

**PROPODIAL ELABORATION IN SOUTHERN AFRICAN AND INDIAN
OCEAN FISSURELLIDAE (MOLLUSCA: PROSOBRANCHIA)
WITH DESCRIPTIONS OF TWO NEW GENERA
AND ONE NEW SPECIES**

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ABSTRACT. Species previously assigned to *Amblychilepas* Pilsbry, 1890, in southwestern, southern, and eastern Africa and the western Indian Ocean are reviewed. *Amblychilepas* has an unmodified propodium and is represented in southern Africa by *A. platyactis*, new species. Two kinds of elaborate propodial processes form the basis for new genera. *Dendrofissurella*, type species *Patella scutellum* Gmelin, 1791, from southern Africa, has a large body and a trunklike propodium with side branches. The genus is monotypic, although two subspecies are recognized. *Medusafissurella*, type species *Fissurella salebrosa* Reeve, 1850, has a smaller body and a propodium of radiating tentacles. Three species are known: *M. salebrosa* (Reeve), in the Arabian Sea and east Africa, *M. dubia* (Reeve, 1849), in southern and eastern Africa, and *M. chemnitzii* (Sowerby, 1835) in southwestern Africa. The function of the propodium remains to be investigated.

INTRODUCTION

The propodium (anterior end of the foot) in fissurellids has not heretofore been reported to have unusual features. Here we describe elaborate propodial tentacles in four fissurellid species occurring in the Arabian Sea, and along the eastern, southern, and southwestern coasts of Africa. These species were previously assigned to *Amblychilepas* Pilsbry, 1890, the type species of which lacks these processes. Two genera are proposed, each strikingly different in shell and body proportions, as well as propodial elaboration. Three of the species are poorly known and have rarely been discussed subsequent to their original descriptions.

The genera treated here (*Amblychilepas*, *Medusafissurella*, new genus, and *Dendrofissurella*, new genus) are closely related in radular and shell characters and are assigned to the subfamily Fissurellinae. We follow Thiele (1929) and McLean (1984a, 1984b) in recognizing two subfamilies in the Fissurellidae: Emarginulinae and Fissurellinae. The Emarginulinae are the oldest, originating in the Mesozoic. Despite major

differences among genera in shell characters, the radula in the Emarginulinae has unifying features; further subdivisions are therefore recognized only at the tribal level. The relatively few genera in the Fissurellinae are relatively young, appearing in the Cenozoic.

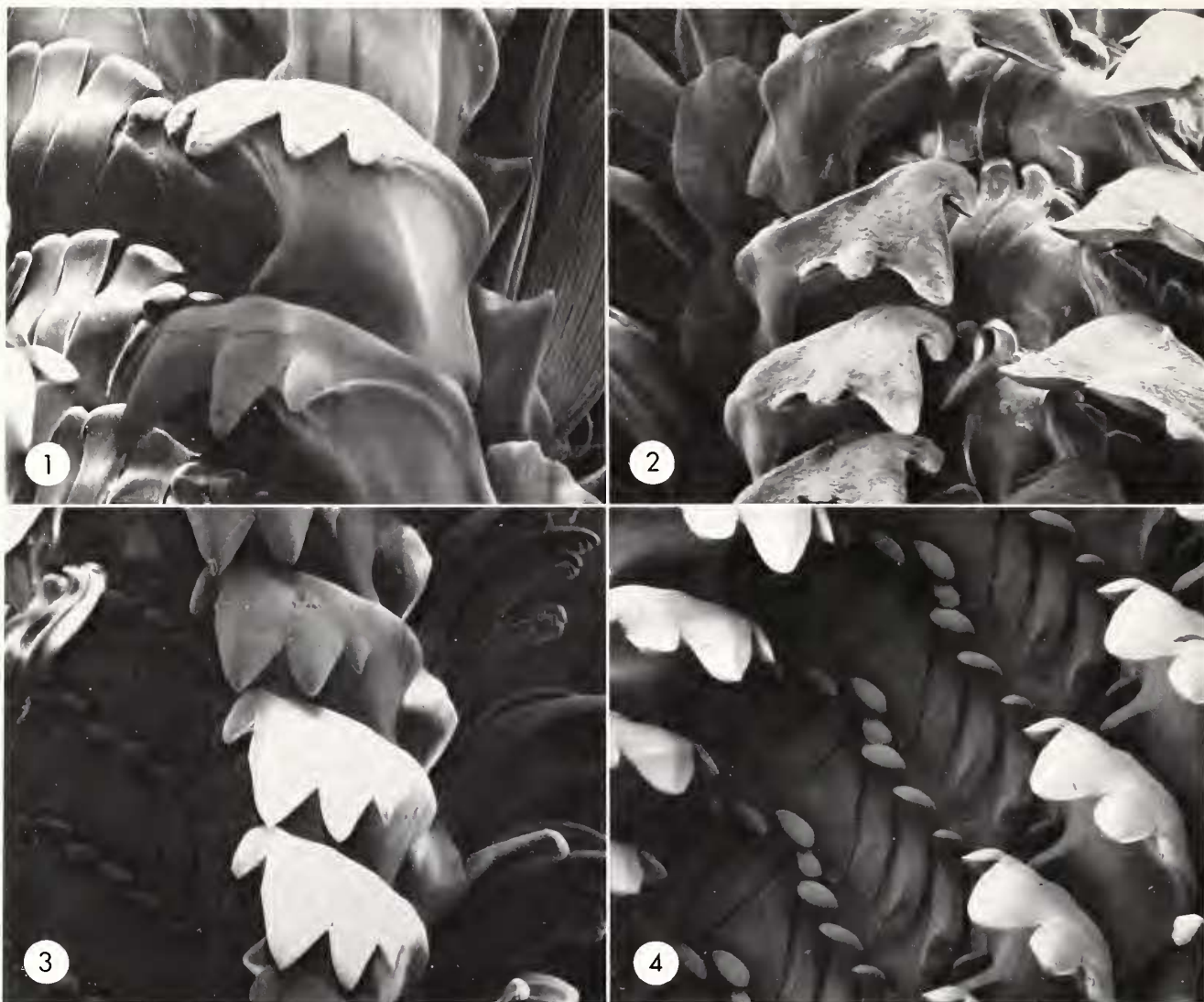
Fissurelline genera differ from emarginuline genera in the following features: 1) the rachidian plate of the radula has a broad base and a narrow tip, rather than the broad or moderately broad tip of the emarginuline rachidian; 2) the large outer lateral tooth is so long that it is aligned with the inner lateral teeth of the row above, rather than the same row as in emarginuline genera (Hickman, 1984); 3) the shell muscle lacks the inwardly directed hook-shaped process of emarginuline genera (Odhner, 1932); 4) the selenizone that is present at least in the early juvenile of emarginuline genera is lacking (McLean, 1984a, 1984b).

This paper treats those fissurelline genera in which the body tends to be larger than the shell. Shells in this group have been confused with emarginuline genera in the tribe Fissurellidini; the latter—*Lucapinella* Pilsbry, 1890; *Leurolepas* McLean, 1970; *Fissurellidea* Orbigny, 1841; *Pupillaea* Sowerby, 1835; and *Buchanania* Lesson, 1830—were treated by McLean (1984a).

Material upon which this paper is based is housed in the following museums or collections: AMS, Australian Museum, Sydney; BMNH, British Museum (Natural History), London; CAS, California Academy of Sciences, San Francisco; JC, J. Christiaens collection, Hasselt, Belgium; LACM, Los Angeles County Museum of Natural History, Los Angeles; MNHN, Muséum National d'Histoire Naturelle, Paris;

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2. Natal Museum, Pietermaritzburg 3201, Natal, South Africa.



Figures 1–4. SEM views of radulae, showing a narrow rachidian with expanded base, four narrow laterals, a large quadricuspid outer lateral, an uncusped lateromarginal plate, and slender marginals; all $\times 200$. 1. *Medusafissurella dubia* (Reeve, 1849). Salt Rock, Umlahli District, Natal, South Africa, NM B9928. 2. *Dendrofissurella scutellum hiantula* (Lamarck, 1822). Algoa Bay, Eastern Cape Province, South Africa, NM B9919. 3. *Amblychilepas platyactis*, new species. Paratype, Kwelera, Eastern Cape Province, South Africa, NM B9929/T3058. 4. *Fissurella nimbose* (Linnaeus, 1758). Puerte La Cruz, Venezuela, LACM 76-30.

NM, Natal Museum, Pietermaritzburg; USNM, United States National Museum, Washington, D.C.

Family Fissurellidae Subfamily Fissurellinae

Three genera having no reported modification of the propodium are currently recognized in the subfamily Fissurellinae: 1) *Fissurella* Bruguière, 1798 (with several subgenera), in which the size of the body does not greatly exceed that of the shell and the large outer lateral radular plate has four cusps; 2) *Amblychilepas* Pilsbry, 1890, with an oval shell, central foramen, and large body; the large outer lateral has

four cusps as in *Fissurella*; 3) *Macrochisma* Sowerby, 1839 (with several subgenera), in which the shell is narrow, the foramen is elongate and posterior, the body much longer than the shell and the large outer lateral has three cusps (one very small); Kilburn has noted (unpublished observation) that *Macrochisma africana* Tomlin, 1932, has a deeply bifid propodium. McLean (1970) included the monotypic genus *Leurolepas* McLean, 1970, in the Fissurellinae, but later (1984a) transferred it to the Emarginulinae, tribe Fissurellidini.

Radulae within the Fissurellinae show few generic and specific differences. Radulae of members of four genera (*Fissurella*, *Amblychilepas*, *Medusafissurella*, and *Dendrofissurella*) are illustrated here (Figs. 1–4). Each has a narrow rachidian with expanded base, four narrow laterals, a large

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quadricuspid outer lateral, an uncusped lateromarginal plate, and slender marginals. The marked asymmetry of the fissurellid radula, which places the laterals of the left side of the ribbon higher than those of the right, has been discussed by Hickman (1981).

The five genera (two new) here recognized in the subfamily Fissurellinae may be keyed as follows:

- 1a. Propodium without tentacles 2
- b. Propodium with elaborate tentacles 4
- 2a. Body not or not greatly exceeding size of shell *Fissurella*
- b. Body at least twice shell length 3
- 3a. Foramen oval, central *Amblychilepas*
- b. Foramen elongate, posterior *Macrochisma*
- 4a. Propodium with numerous subequal tentacles *Medusafissurella*
- b. Propodial outgrowth with main trunk and side branches *Dendrofissurella*

Medusafissurella new genus

Type species: *Fissurella salebrosa* Reeve, 1850. Recent, Arabian Sea, Indian Ocean.

DESCRIPTION. Shell markedly narrowed anteriorly; anterior end raised; anterior shell edge thinner and sharper than elsewhere; posterior end only slightly or not at all raised; anterior slope concave. Foramen oval, interior callus not truncated posteriorly. Sculpture of strong, scabrous ribs. Posterior portion of foot covered by shell; shell edge only slightly enveloped by mantle folds; propodium with radiating tentacles, sometimes branched, subequal in length. Large outer lateral tooth of radula quadricuspid.

REMARKS. On the basis of shell characters alone, the species grouped here have been variously assigned to other fissurellid genera. The shell of *Medusafissurella* differs from that of most *Fissurella* species in having a prominently raised anterior end with thin edge, and from *Amblychilepas* and *Dendrofissurella* in having strong, scabrous primary ribs, and a less raised posterior end. Body differing in being nearly covered by the shell and in having numerous propodial tentacles, not the single main, branching structure of *Dendrofissurella*.

The quadricuspid outer lateral tooth of *Medusafissurella* is similar to that in *Dendrofissurella*, *Amblychilepas*, and *Fissurella*.

Medusafissurella comprises three allopatric species: *M. salebrosa* (Reeve, 1850), *M. dubia* (Reeve, 1849), and *M. chemnitzii* (Sowerby, 1835).

ETYMOLOGY. The prefix is suggested by the propodial tentacles, which recall the serpentine locks of Medusa in Roman mythology; gender feminine.

Medusafissurella salebrosa (Reeve, 1850)

Figures 5–7, 14, 26

Fissurella salebrosa Reeve, 1850:pl. 11, sp. 78; Bosch and Bosch, 1982:29, 3 figs. Type locality: Karachi, Pakistan.

Glyphis salebrosa; Pilsbry, 1890:208, pl. 39, fig. 7 [copy Reeve, 1850:fig. 78].

Diodora salebrosa; Christiaens, 1974:91.

Lucapinella salebrosa; Biggs, 1969:202 [checklist only].

“*Fissurella subrostrata* Guilding”; of Sowerby II, 1862:192, fig. 215, not *F. subrostrata* “Gray”; Sowerby, 1835b:6, fig. 35.

DESCRIPTION. Shell markedly narrowed anteriorly; anterior end raised; anterior slope concave; sculpture of strong, scabrous ribs; rib interspaces broad, foramen nearly circular, broader posteriorly. Posterior portion of foot covered by shell, shell edge only slightly enveloped by mantle folds; exterior color gray-brown, interior white. Propodium with about 15 radiating tentacles, subequal in size, anteriormost the largest. Maximum shell length 35 mm (JC colln.).

The description of the propodium is based on the only preserved specimen available (CAS 031984, Figs. 14, 26).

TYPE MATERIAL. Lectotype here designated, BMNH 1975078 (Fig. 5), one of two original syntypes so catalogued.

DISTRIBUTION. Indian Ocean, northernmost Arabian Sea, Pakistan to Somalia.

MATERIAL EXAMINED. PAKISTAN: Bulejji Point, Sind Province (LACM 79-34) (Fig. 6); Goth Jafar, west of Karachi (CAS 031984) (Figs. 14, 26); Karachi (NM H5382). OMAN: Muscat (JC colln.); Masirah Island (NM J3845). SOMALIA: Alula (JC colln.); Socotra Island (JC colln.) (Fig. 7).

COMPARISONS. The anterior end of *M. salebrosa* is more tapering and the primary ribs are more strongly defined and broadly separated than those of *M. dubia* and *M. chemnitzii*.

REMARKS. This enigmatic species is poorly known, partly because of its localized distribution. The first illustration with a properly documented locality subsequent to that of Reeve’s original figure is that of Bosch and Bosch (1982), who indicated it as common, “distributed generally on rocks or in crevices.”

Sowerby II (1862) incorrectly placed *F. salebrosa* in the synonymy of *F. subrostrata* “Guilding,” Sowerby, 1835, a yet unrecognized taxon (see synonymy above), said to be from St. Vincents, West Indies. The original illustration shows more numerous, less pronounced radial ribs than those of *F. salebrosa*. Christiaens (1973:91) tentatively placed *F. salebrosa* in the synonymy of *F. subrostrata*. He now considers (pers. comm.) the specimen figured by Perez-Farfante (1943: 20, pl. 6, figs. 9–11) as “*F. subrostrata*” to be a mislocalized specimen of *Medusafissurella salebrosa*.

Medusafissurella dubia (Reeve, 1849)

Figures 1, 8–10, 15

Fissurella dubia Reeve, 1849:pl. 6, fig. 35. Type locality: Port Natal [= Durban], South Africa.

Lucapina dubia; Sowerby II, 1862:193, pl. 9, fig. 208.

Glyphis dubia; Pilsbry, 1890:217, pl. 39, fig. 6 [copy Reeve, 1849:fig. 35].

Amblychilepas dubia; Kilburn and Rippey, 1982:35, pl. 6, fig. 2.

Fissurellidea genevieveae Dautzenberg, 1929:546, pl. 1, figs. 3–7. Type locality: Madagascar (several localities cited).

DESCRIPTION. Shell outline oval, slightly narrowed anteriorly; anterior end raised, concave at early stage, all slopes convex at later stage. Sculpture of strong scabrous ribs, rib interspaces relatively narrow; foramen oval. Posterior portion of foot covered by shell, shell edge slightly enveloped by mantle folds. Propodial tentacles approximately 12 on ventral side, some branching up to 4 times so that 2 or 3 layers of tentacles project in anterior view. Maximum shell length 36 mm (Kilburn and Rippey, 1982).

The description of the animal is based on preserved specimens from Salt Rock, Umhlali District, Natal (NM B9915) (Fig. 15), collected by R.N. Kilburn, November, 1970.

TYPE MATERIAL. Holotype, BMNH 198495 (Fig. 9). Type material of *Fissurellidea genevieveae* has not been located. It is not in the Dautzenberg collection at the Brussels Museum.

DISTRIBUTION. East Africa to South Africa: Mogadiscio, Somalia, to Kelso, Natal, South Africa; Madagascar. Living in submerged rock crevices, intertidal fringe to a depth of several meters.

MATERIAL EXAMINED. SOMALIA: Mogadiscio (USNM 673793; LACM 25051); Socotra Island (JC colln.). MOZAMBIQUE: Bazaruto Island, near lighthouse (NM G4599) (Fig. 8); Cabo de Santa Maria, Bay of Maputo (NM 6238); Mozambique (LACM 25206). SOUTH AFRICA, NATAL: Kosi Bay, Zululand (NM B2092); Mvoti River mouth (NM 9350); 3 mi. off Umhlanga Rocks, 12–13 fm. (NM A269); Salt Rock, Umhlali district (NM B9928) (Fig. 15); Tongaat (NM 7132); Durban (NM 9489, NM B2093, NM 8989, NM 267, NM 7139, NM 9004) (Fig. 10); Isipingo (NM 5883); Umkomaas (NM 9132); Park Rynie (NM 5870); Kelso (NM B2095).

COMPARISONS. Shell differing from that of *M. salebroso* in having a less tapered anterior end, a greater number of radial ribs, a more elongate foramen; propodium differing in having the tentacles branched.

REMARKS. Kilburn and Rippey (1982) were the first to recognize the occurrence of this species subsequent to the original description of Reeve. They noted that it differed anatomically from “*Amblychilepas*” *scutellum* but did not provide details. *Fissurellidea genevieveae* Dautzenberg has not been noticed in subsequent literature, but the original figures are adequate to allocate it to *Medusafissurella dubia*, with which it was not originally compared.

Medusafissurella chemnitzii (Sowerby, 1835)

Figures 11–13, 16

Fissurella chemnitzii Sowerby, 1835a:126; Sowerby, 1835b: 5, fig. 55; Reeve, 1849:pl. 1, fig. 1 (part). Original locality unknown [“Benguela, West Africa,” cited by Reeve, 1849].

Fissurellidea chemnitzii; Sowerby II, 1862:202, pl. 2, fig. 29, pl. 8, fig. 192 (part).

Megatebennus (section *Amblychilepas*) *chemnitzii*; Pilsbry, 1890:185, pl. 39, fig. 90 [copy Reeve, 1849:fig. 1].

DESCRIPTION. Shell outline oval, slightly narrowed anteriorly; anterior end markedly raised; posterior end slightly raised. All slopes straight to slightly concave. Sculpture of strong irregular, finely scabrous ribs; rib interspaces narrow. Foramen elongate oval. Posterior portion of foot projecting ¼ shell length beyond shell, shell edge slightly enveloped by mantle folds. Propodial tentacles numerous, irregular. Maximum shell length 52 mm (East London Museum 11001).

The description of the animal is based on four poorly preserved specimens from Baia de Santa Maria, Benguela Prov., Angola (MNHN uncat.), collected by S. Gofas, December, 1982 (Figs. 12, 16).

TYPE MATERIAL. Neotype (here designated), MNHN uncat., Baia de Santa Maria, Angola (Fig. 12). Dimensions: 24.8 × 15.2 × 7.2 mm. Sowerby’s original material is unknown; it has not been recognized in the British Museum.

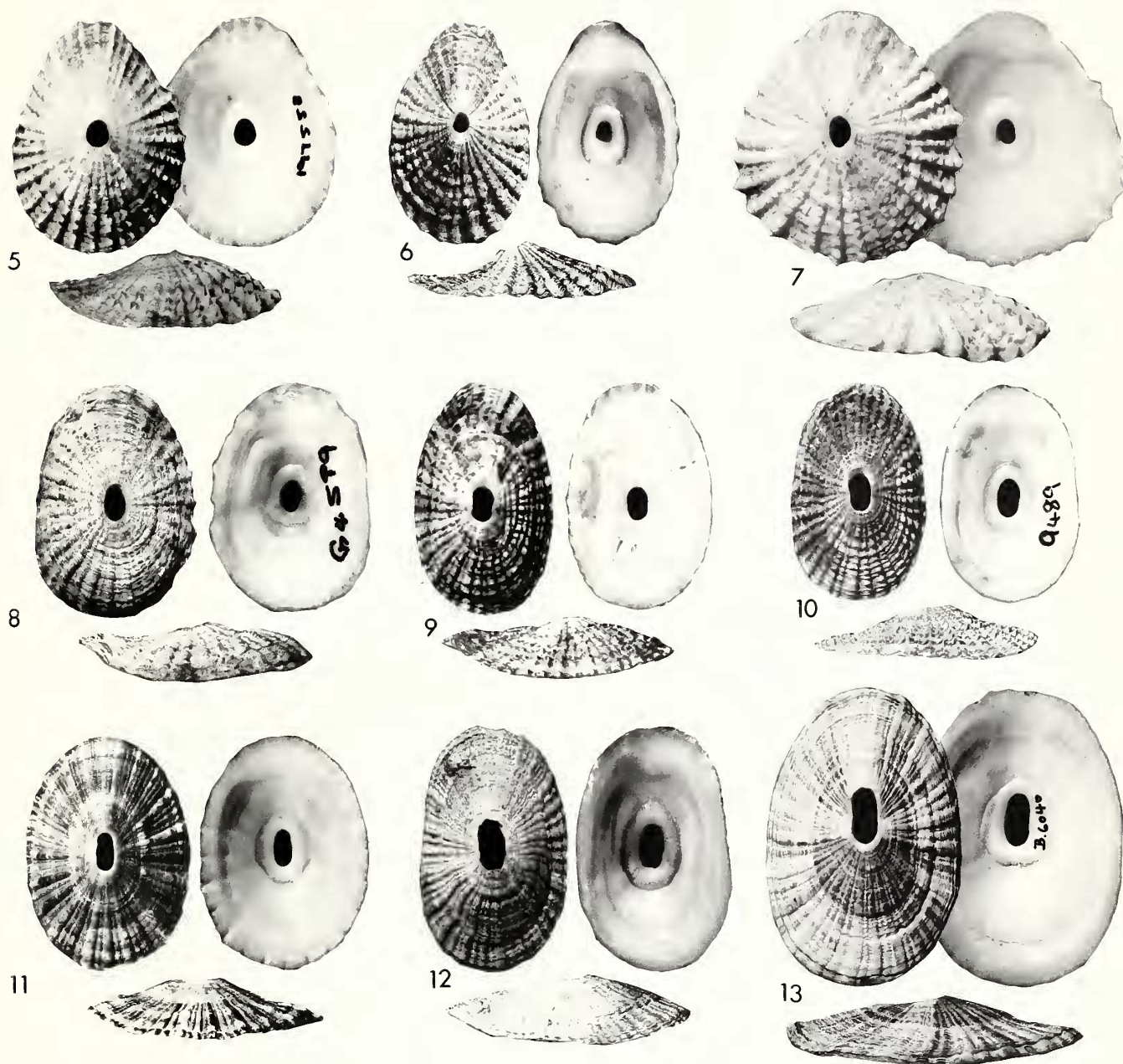
DISTRIBUTION. Southwestern Africa: Pointe Noire, Congo, to Kunene River Mouth, Angola/Namibia border. Rocky intertidal to 2 m.

MATERIAL EXAMINED. CONGO: Pointe Noire, Côte Sauvage (JC colln.) (Fig. 11). ANGOLA (all MNHN uncat., collected by S. Gofas): Ambrizete, Zaire Prov.; Baia de Santa Maria, Benguela Prov. (Figs. 12, 16); Sao Nicolau, Mocamedes Prov.; Chapeu Armado, Mocamedes Prov.; Luanda, Luanda Prov. (JC colln.). NAMIBIA: Kunene River mouth (NM B6040; East London Museum 11001) (Fig. 13).

COMPARISONS. *Medusafissurella chemnitzii* differs from *M. salebroso* and *M. dubia* in its larger size, more elongate foramen, less scabrous ribs, and in having red rather than brown or gray coloration.

REMARKS. This is the most enigmatic of the three *Medusafissurella* species. A neotype is here designated because original material cannot be located and none of the illustrations purported to represent this species are completely accurate. The history of the name *Fissurella chemnitzii* is detailed below.

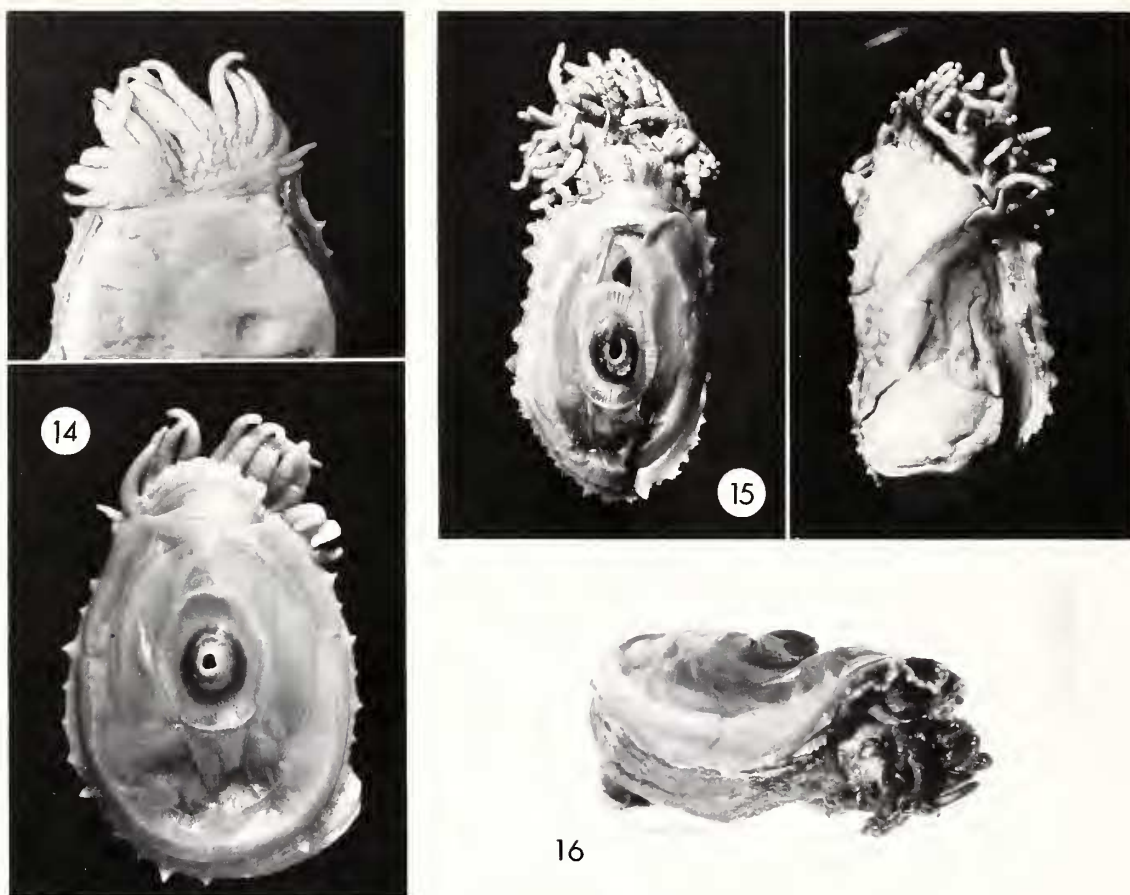
The descriptions of Sowerby (1835a) and Reeve (1849) agree with the species as here interpreted. Sowerby (1835a) remarked that “the only specimen I have ever seen of this species was in the Tankerville Collection, from which after several vicissitudes, it has at length found its way to Mr. Cuming’s.” Although he also noted: “This remarkable shell is represented by Martini (I, t. xi, fig. 100),” the shell illustrated by Sowerby (1835b) is not copied from Martini’s figure 100 (Martini and Chemnitz, 1769–1795) (which we consider to represent the Mediterranean *Diodora italica* (Defrance, 1820)), but could only be the Tankerville shell. The original figure of Sowerby (1835b) does not show the primary ribs as sufficiently prominent and the foramen is somewhat too large; however, the proportions are correct and it conceivably could



Figures 5–13. Shells of *Medusafissurella* species; exterior and interior views with anterior at top; lateral views of left side. **Figs. 5–7.** *M. salebroza* (Reeve, 1850). **5.** Lectotype, Karachi, Pakistan, BMNH 1975078, 27.0 × 20.7 × 8.9 mm. **6.** 7 km WNW Buleiji Point, Sind Province, Pakistan, LACM 79-34, 20.0 × 12.5 × 5.4 mm. **7.** Socotra Island, Somalia, JC colln., 29.2 × 26.7 × 10.2 mm. **Figs. 8–10.** *M. dubia* (Reeve, 1849). **8.** Bazaruto Island, Mozambique, NM G4599, 22.4 × 15.5 × 4.0 mm. **9.** Holotype, Durban, Natal, South Africa, BMNH 1984195, 22.1 × 13.7 × 5.3 mm. **10.** Durban, NM 9489, 19.4 × 12.1 × 4.6 mm. **Figs. 11–13.** *M. chemnitzii* (Sowerby, 1835). **11.** Pointe Noire, Côte Sauvage, Congo, JC colln., 23.1 × 16.4 × 5.9 mm. **12.** Neotype, Baía de Santa Maria, Angola, MNHN uncat., 24.8 × 15.2 × 7.2 mm. **13.** Kunene River Mouth, Namibia, NM B6040, 42.9 × 28.9 × 10.7 mm.

have been based on the species treated here. The specimen figured by Reeve from “Benguela, West Africa, collected by Dr. Tams” has not been located in the British Museum; this illustration is inaccurate because it depicts primary ribs that

are too prominent, too few, and with interspaces too broad, and a foramen that is broader posteriorly. A later illustration (Sowerby II, 1862), which has no documentation, is based on a still different specimen; in fact, it is a better rendition



Figures 14–16. Preserved bodies of *Medusafissurella* species. **14.** *M. salebrosa*, dorsal and ventral views of preserved body out of shell, Goth Jafar, 10 mi. west of Karachi, Pakistan, CAS 031984, shell dimensions $26.5 \times 20.0 \times 9.6$ mm. **15.** *M. dubia*, dorsal and ventral views of preserved body out of shell, Salt Rock, Umhlali Dist., Natal, South Africa, NM B9928, shell dimensions $29.0 \times 16.9 \times 7.2$ mm. **16.** *M. chennitzii*, Baia de Santa Maria, Angola, MNHN uncat., lateral view of preserved specimen, shell dimensions $27.7 \times 16.5 \times 7.5$ mm.

of *M. dubia* than anything else. Despite these discrepancies, we retain the name of Sowerby (1835), basing it on his description (1835a) and his figure (1835b), to which we relate the neotype specimen designated here.

Dendrofissurella new genus

Type species: *Patella scutellum* Gmelin, 1791. Recent, southern Africa.

DESCRIPTION. Shell oval, anterior end narrower than posterior, ends raised; foramen nearly central, elongate-oval. Sculpture of fine radial ribs. Foot projecting posterior to shell for distance greater than length of shell; shell edge slightly enveloped by mantle fold; propodium with single tapering, trunklike elongation, with approximately 9 irregularly placed lateral branches. Large outer lateral tooth of radula quadricuspid.

REMARKS. Differing from *Amblychilepas* in having an elaborate propodium, minimal envelopment of the shell by the mantle, and minor development of the papillae of the

upper lobe of the mantle. Differing from *Medusafissurella* in having a trunklike propodium rather than a broad propodium with subequal tentacles. The foot projects posteriorly to a greater extent than in *Medusafissurella*.

The quadricuspid outer lateral tooth of *Dendrofissurella scutellum* is similar to that of species of *Fissurella*, *Amblychilepas*, and *Medusafissurella*.

The genus contains a single species, for which we recognize two geographic subspecies.

ETYMOLOGY. The prefix is suggested by the trunklike propodium, a Greek word for tree; gender feminine.

Dendrofissurella scutellum (Gmelin, 1791)

(a) *D. scutellum scutellum*

Figures 17, 18

Patella scutellum Gmelin, 1791:3731. Original locality unknown [Table Bay, designated by Kilburn and Rippey, 1982:211].

Fissurella scutellum; Krauss, 1848:63.

Megatebennus (section *Amblychilepas*) *scutellum*; Pilsbry, 1890:184, pl. 39, fig. 89, pl. 44, figs. 99, 100, 1, 2.
Fissurellidae *scutella* [sic]; Turton, 1932:207.
Amblychilepas scutella [sic]; Barnard, 1963:286, figs. 21b, 22d–f.
Amblychilepas scutellum; Kensley, 1973:29, fig. 30 [drawing of animal]; Tietz and Robinson, 1974:48, pl. 26 [photograph of animal].
Amblychilepas scutellum scutellum; Kilburn and Rippey, 1982:35, 212, pl. 6, fig. 1 (part).
Not *Fissurella scutella* of Reeve, 1849:pl. 6, fig. 33 [= *A. javanicensis* (Lamarck)].
Not *Fissurellidea scutella* of Sowerby II, 1862:203, pl. 9, fig. 207 [= *A. javanicensis* (Lamarck)].
Fissurellidea sella Sowerby, II, 1862:203, pl. 8, fig. 197; Turton, 1932:207. Type locality: “South Africa.”
Megatebennus (section *Amblychilepas*) *sella*; Pilsbry, 1890:185, pl. 62, fig. 3 [copy Sowerby II].

(b) *D. scutellum hiantula* (Lamarck, 1822)

Figures 2, 19–22

Fissurella hiantula Lamarck, 1822:14; Mermod, 1950:708, figs. 18.1, 18.2, 18.3 [syntypes, Lamarck Collection]. Type locality: “Mer des Indes” [Algoa Bay, here designated].
Fissurellidea hiantula; Sowerby II, 1862:202, pl. 8, figs. 193–195.
Not *Fissurellidea hiantula* of Pilsbry, 1890:179, or other authors treating species from Argentina [= *Fissurellidea megatrema* Orbigny, 1841].
Amblychilepas scutellum hiantula; Kilburn and Rippey, 1982:35, 211, pl. 6, fig. 1 (part).
Fissurella incarnata Krauss, 1848:65, pl. 4, fig. 7; Janus, 1961:3, pl. 1, figs. 4–6. Type locality: “In sinu tabulari et falso, in litore natalensi.”
Fissurellidea incarnata; Sowerby II, 1862:203, pl. 8, fig. 109.
Megatebennus (section *Amblychilepas*) *incarnata*; Pilsbry, 1890:186, pl. 35, figs. 4, 5 [copy Krauss].
Fissurellidea incarnata maculata Turton, 1932:206, pl. 53, fig. 1431. Type locality: Port Alfred.
Fissurellidea multilineata Turton, 1932:206, pl. 53, fig. 1432. Type locality: Port Alfred.
Fissurellidea albanyana Turton, 1932:207, pl. 54, fig. 1433. Type locality: Port Alfred.
Fissurellidea nigrostrigata Turton, 1932:207, pl. 54, fig. 1435. Type locality: Port Alfred.

DESCRIPTION. Shell saddle-shaped, anterior and posterior ends raised; sculpture of fine raised ribs of nearly equal size, but with some ribs twice the width of adjacent ribs.

Following Kilburn and Rippey (1982), we recognize two geographic subspecies, with distributions overlapping in False Bay, where they intergrade. To the west (on the cold temperate Atlantic coast) occurs the typical *D. scutellum scutellum*, which has a large thick shell (attaining 40 to 50 mm in length) with moderately to extremely raised ends, and a drab pattern of dark gray to olive-brown. To the east (on the warm temperate south coast) it is replaced by *D. scutellum hiantula*,

which is smaller (length 30 mm or less), thinner-shelled, with ends less raised, and a more vividly and delicately colored pattern, generally pink or brown with white rays or spots.

TYPE MATERIAL. As noted by Pilsbry (1890) and Kilburn and Rippey (1982:211), Gmelin (1791) cited a clearly recognizable figure of Meuschen (1782:pl. 2, fig. 3) to represent *Patella scutellum*. Meuschen’s illustration is a type figure; a type specimen is not available.

There are three specimens labeled *Fissurella hiantula* in the Lamarck collection, as discussed by Mermod (1950). These specimens clearly relate the name to the eastern subspecies of *D. scutellum*. Of three syntypes figured by Mermod, specimen number 1, at 31 mm in length, is close to Lamarck’s cited dimensions. Lamarck’s (1822) reference to an illustration of Born (which we now identify as *Pupillaea aperta* (Sowerby, 1825)) is discounted because type material of *F. hiantula* is available.

Type material for *F. incarnata* Krauss, was not located by Janus (1961), who designated a neotype in the Stuttgart Museum. Janus selected a specimen that agrees with our concept of *F. scutellum scutellum*, but Krauss’s figures agree with *F. scutellum hiantula*. We therefore retain the name in the synonymy of *F. scutellum hiantula*.

The holotype of *Fissurellidea sella*, from “South Africa” is in the BMNH.

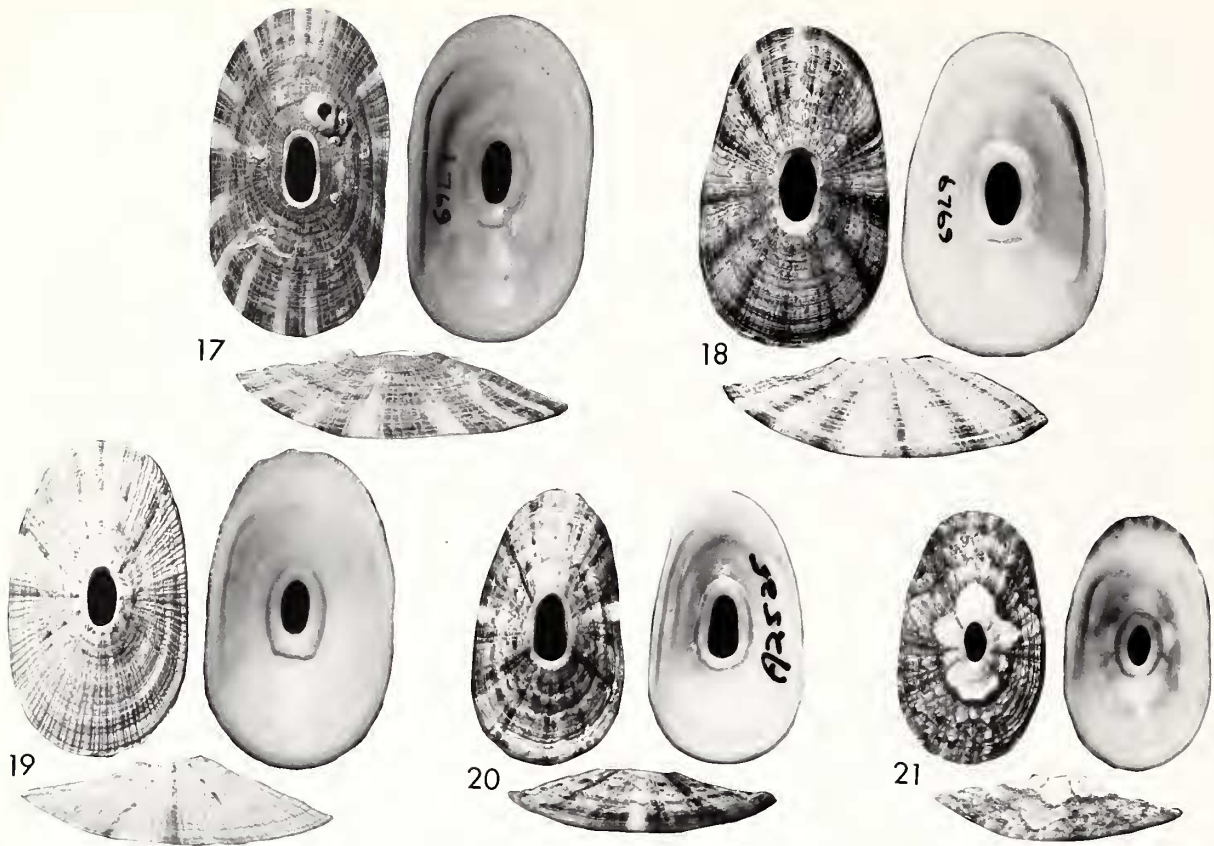
Turton’s types, all from Port Alfred, are in the Oxford University Museum.

DISTRIBUTION. South Africa: Natal North Coast to Saldanha Bay, Cape Province.

Shells of both subspecies are well represented in museum collections from numerous localities. The following preserved specimens of the typical subspecies have been examined: Saldanha Bay (NM B9918); Table Bay (NM B9917); Cape Town (LACM 25203). These specimens tend to have the propodium contracted, some to the point of nearly concealing the feature. Preserved specimens of *D. scutellum hiantula* are scarce in museum collections. Our evidence that the eastern subspecies has a propodium similar to that of *D. scutellum* is based on: 1) the specimen illustrated by Tietz and Robinson (1974:pl. 46), presumably from the Tsitsikama coast, which shows a pink, rather than drab shell, as expected in the eastern subspecies; 2) a single specimen from Still Bay (NM A2536), which has an intact, dried animal with well-developed propodium; and 3) three preserved specimens from Algoa Bay (NM B9919).

Some specimens provisionally identified as *D. scutellum hiantula* have fewer ribs overall and have ribbing of alternating strength (Figs. 20, 21). Color variation is similar to that of *D. scutellum hiantula*. Until preserved specimens become available, the identity of this form is not certain. It could be a variant of this species, or it could prove to be yet another species of *Amblychilepas*.

MATERIAL EXAMINED. (a) *D. scutellum scutellum*: SOUTH AFRICA: Saldanha Bay (NM 5584); Shell Bay (NM 8725); various localities in Table Bay (NM 6381, NM 1271, NM 6641, NM A2975); Kommetjie, west coast Cape Peninsula (NM 5586, NM A4189). Simonstown, shallow dredgings (NM 8976, NM 6769) (Figs. 17, 18); Strandfontein, False



Figures 17–21. Shells of *Dendrofissurella* species; exterior and interior views with anterior at top; lateral views of left side. **Figs. 17, 18.** *Dendrofissurella scutellum scutellum* (Gmelin, 1791). **17.** Simonstown, False Bay, Western Cape Province, South Africa, NM 6769, $33.7 \times 18.8 \times 8.4$ mm. **18.** Same lot, $32.5 \times 19.8 \times 9.8$ mm. **Figs. 19–21.** *D. scutellum hiantula* (Lamarck, 1822). **19.** East London, Eastern Cape Province, South Africa, NM A4186, $30.0 \times 17.6 \times 8.0$ mm. **20.** Cape Agulhas, Western Cape Province, South Africa, NM A2535, $20.0 \times 11.6 \times 4.8$ mm. **21.** Port Elizabeth, Eastern Cape Province, South Africa, LACM 3765, $15.0 \times 8.8 \times 3.9$ mm.

Bay (NM A3961); off Macassar Beach, False Bay, 10 fm. (NM A3123).

(b) *D. scutellum hiantula*: SOUTH AFRICA, CAPE PROVINCE: Cape Agulhas (NM A2535); Still Bay (NM A2536, NM A2531); Mossel Bay (NM A5307); Jeffreys Bay (NM 5886, NM B6143); Algoa Bay (NM B2868, NM B1795, B439); Port Alfred (NM B440-2, NM B6142, NM B6355); East London (NM A4186, NM 8363) (Fig. 19). TRANSKEI: Kei River mouth (NM C3476); Nxaxo River mouth (NM C3773); Qolora River mouth (NM C3406); Sandy Point (NM C3665); Dwesa (NM C5961); Lwandile/Mdumbi (NM C75); Hluleka (NM C1500); Coffee Bay (NM A801, NM B6139); Nthlonyane (NM B1430); Mkambati (NM C5608); Mbotyi (NM A2534); Mzamba (NM B4550, NM 7142). NATAL: Port Shepstone (NM 8986, NM 9128); Kelso (NM 5885); Mtwalume (NM B8605); Umkomaas (NM 1273, NM 7151); Durban (NM B4884); Tongaat (NM 71411); 3 mi. off Umhlanga Rocks, 12–13 fm. (NM A272); Umhlali beach (NM A4575); Mvoti River mouth (NM 7144).

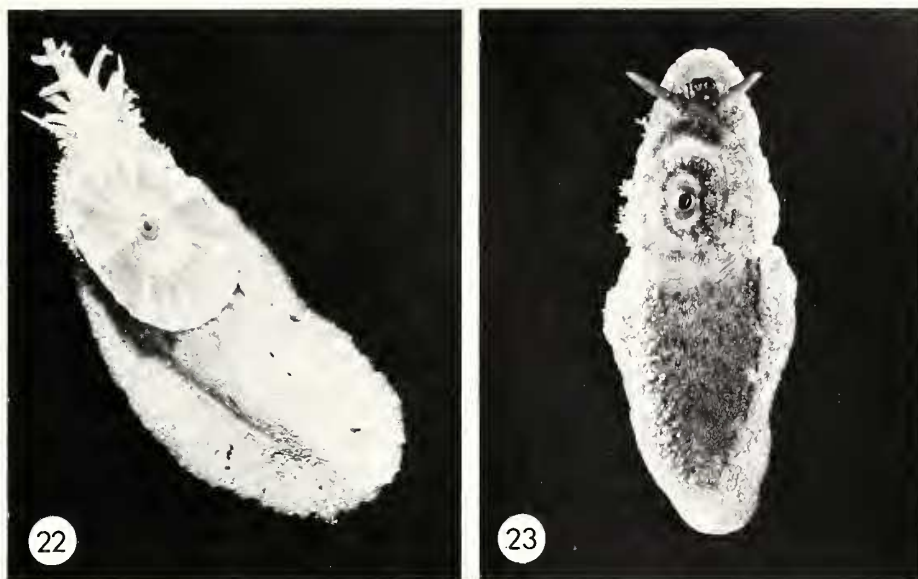
COMPARISONS. On shell characters both subspecies of *D. scutellum* differ from the three species of *Medusafissurella* in having less prominent, nonscabrous ribs and in having the posterior end more raised.

REMARKS. Reeve (1849) and Sowerby II (1862) incorrectly considered *F. scutellum* an earlier name for the Australian *A. javanicensis*; their figures show the latter. Krauss (1848) and Barnard (1963) used *A. scutellum* for the South African species, but incorrectly placed *A. javanicensis* in its synonymy. Pilsbry (1890) erroneously used the name *Fissurellidea hiantula* for an Argentinean species, which McLean (1984a) relegated to the synonymy of *Fissurellidea megatrema* Orbigny, 1841.

The prominent dendritic propodium of *D. scutellum* has previously been figured by Kensley (1973) and by Tietz and Robinson (1974); the latter figure is reproduced here (Fig. 22). Kensley (1973) illustrated a bifurcation in the propodium, although all specimens that we have examined have a single central trunk.

Genus *Amblychilepas* Pilsbry, 1890

Amblychilepas Pilsbry, 1890:184. Type species: *Fissurella trapezina* Sowerby, 1835 (= *F. javanicensis* Lamarck, 1822). Recent, Australia.



Figures 22, 23. Living animals of *Dendrofissurella* and *Amblychilepas*. **22.** *Dendrofissurella scutum hiantula*, dorsal view of living animal, Tsitsikama Coastal National Park, Eastern Cape Province, South Africa; overall length about 80 mm; after Tietz and Robinson (1974). **23.** *Amblychilepas nigrita* (Sowerby, 1835), dorsal view of living animal, New South Wales, Australia, overall length about 80 mm; photograph by John Fields, courtesy AMS.

Sophismalepis Iredale, 1924:219. Type species: *Fissurella nigrita* Sowerby, 1835. Recent, Australia.

DESCRIPTION. Shell oval, anterior end narrower than posterior, ends raised; sculpture of radial striae; foramen nearly central, elongate oval. Foot projecting posterior to shell for distance greater than length of shell; shell edge enveloped by upper fold of mantle, from which long papillae extend toward foramen; propodium unmodified. Massive outer tooth of radula quadricuspid.

REMARKS. Except for *A. platyactis* new species, species of *Amblychilepas* are restricted to Australia. Figured here for comparison (Fig. 23) is a living animal of the Australian *A. nigrita* (Sowerby, 1835). As in the new species here described, the papillae of the upper fold of the mantle of *A. nigrita* are well developed and project toward the foramen. The propodium of the Australian type species (*A. javanicensis*) is unmodified (based on AMS C.117375).

The following species has been confused with the common south African species here reassigned to *Dendrofissurella scutellum hiantula*.

Amblychilepas platyactis new species

Figures 3, 24, 25

Amblychilepas scutellum [non Gmelin, 1791]; Odhner, 1932: 298, fig. 31 [drawing of animal].

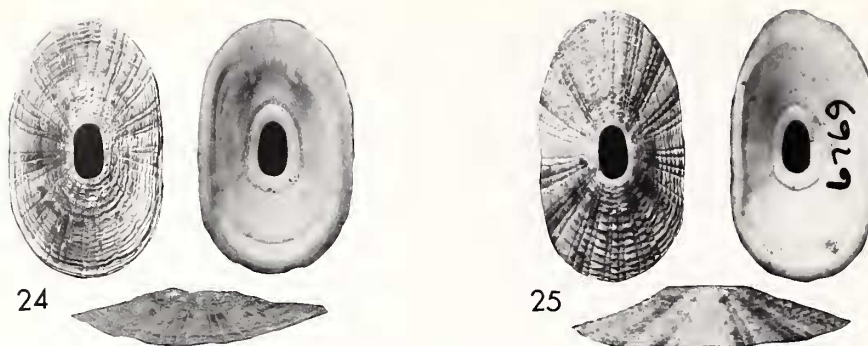
DIAGNOSIS. Shell to 30 mm in length, saddle-shaped, narrowed anteriorly; anterior markedly raised; posterior slightly raised; radial ribs alternating in strength, separated by deeply incised grooves. Primary ribs broad, low, and flat-

topped, up to twice as broad as secondary ribs and 3 times broader than tertiary ribs; primary ribs broader on sides of shell than on ends; concentric growth lamellae thin and raised, especially prominent on broad primary ribs. Color dark red with white rays.

Propodium unmodified; body extending posteriorly for one shell length; upper lobe of mantle enveloping edge of shell and having long, elaborate papillae corresponding to broad primary ribs.

DESCRIPTION. Shell outline elongate-oval in dorsal view, slightly narrowed anteriorly; anterior and posterior ends raised, lateral profile of base evenly curved. Radial sculpture of flat-topped ribs separated by narrow incised grooves rather than interspaces. Primary ribs 14, twice as broad as secondary ribs, which in turn are twice as broad as tertiary ribs. Primary ribs at anterior and posterior ends more elevated than those of sides, particularly in early growth stages. Concentric sculpture of thin, raised incremental growth lines, arched upon crossing primary ribs, to a lesser extent on crossing secondary and tertiary ribs. Foramen elongate-oval, slightly broader posteriorly, $\frac{1}{5}$ shell length. Color brick red, with white rays that tend to emerge at later growth stages and correspond to primary ribs. Margin faintly crenulate to correspond with exterior sculpture, shell edge angulate at sides, thinner anteriorly and posteriorly. Callus surrounding foramen faintly outlined in pink, more bluntly terminating posteriorly than anteriorly.

Propodium unmodified, outline of foot elongate-oval, body extending posteriorly for one shell length. Sides of foot with pustulose tubercles; epipodial tentacles of neck weakly developed; mantle lobe with tubercles like those on foot sides but smaller; lower edge of mantle lobe with projecting pa-



Figures 24, 25. *Amblychilepas platyactis*, new species, exterior and interior views with anterior at top; lateral views of left side. 24. Holotype, Port Alfred, Eastern Cape Province, South Africa, NM B6397/T2744, 17.2 × 10.3 × 3.9 mm. 25. Paratype, False Bay, Eastern Cape Province, South Africa, NM 6769/T3009, 20.5 × 11.0 × 4.5 mm.

pillae having numerous projecting points; upper edge of mantle with fewer papillae that are about three times the size of the lower edge papillae, about 14 major papillae altogether, corresponding to broad primary ribs. Major papillae separated by less prominent papillae. Tips of cephalic tentacles reddish in preservative.

DIMENSIONS. Holotype, shell length 17.2, width 10.3, height 3.9 mm. Maximum length 30.8 mm (NM 6769/T3009).

TYPE MATERIAL. Holotype, NM B6397/T2744, Port Alfred, Eastern Cape Province, South Africa, collected by R. Kilburn, 1966 (Fig. 24). Paratype 1, LACM 2108, Port Alfred, collected by E. Warren, July 1912. Paratype 2, NM B9916/T3008, Kommetjie, collected by C.M. Connolly. Paratypes 3–5, NM B9929/T3055, Kwelera, E of East London, collected by C.M. Connolly. Paratypes 6–11, NM 6769/T3009 (Fig. 25) Simonstown, False Bay, collected by C.M. Connolly. Holotype and paratypes wet-preserved, except for paratypes 6–11, shells only.

DISTRIBUTION. South Africa: East London to Kommetjie, Atlantic coast of Cape Peninsula.

COMPARISONS. On anatomical characters, there is no difficulty in distinguishing intact specimens of *A. platyactis* from both subspecies of *Dendrofissurella scutellum*, the former having elaborate papillae on the upper lobe of the mantle and lacking the propodial elaboration; the latter having small, simple papillae on the upper lobe and having the trunklike propodium. Shells, however, closely approach those of *D. scutellum hiantula*, of which there are specimens with broad primary ribs (Figs. 20, 21) up to twice the breadth of the lesser ribs. However, no specimens of *D. scutellum hiantula* are known with the extremely broad ribs of *A. platyactis*, which may be three times the breadth of the lesser ribs. The development of the scaly sculpture on the primary ribs is much more extreme in the young stages of *A. platyactis*. Shells of all specimens are red and white rayed, which indicates that the range of color variation is minimal in *A. platyactis*. The posterior end of the shell of *A. platyactis* is less raised than that of *D. scutellum*.

REMARKS. We name this species with reluctance, considering the large number of synonyms pertaining to *D. scu-*

tellum hiantula. However, original descriptions of all these taxa make no reference to broad ribbing and it is clear that none of them has sculpture to match the type specimens of *A. platyactis*. The specimen figured by Odhner (1932) is presumed to be this species on the basis of lack of propodial development and the papillae of the upper lobe of the mantle.

ETYMOLOGY. The name is Greek, meaning with wide or flat spokes or rays, suggested by the extremely broad ribs of this species.

DISCUSSION. *Dendrofissurella scutellum* (both subspecies) and the three species of *Medusafissurella* have very different expressions of the propodium, here considered diagnostic at the generic level. However, the vexing question of function remains. One might speculate that the propodial tentacles serve to trap or hold food, such as drifting algae. Yet, in these species the snout, which is no larger than in other fissurellid genera, is dorsal to the proportionally longer propodium (Fig. 26). A role in feeding would be more readily understood if these tentacles were attached to the snout instead of the propodium, access to the mouth thereby being closer. In the fissurellids described here, the snout would presumably have to be extended through the tentacles to reach the food, but the propodium is not bifid, as would be expected if this were the case. Yet, the mouth and the snout are more laterally compressed than in fissurellid genera lacking the propodium.

Stomach contents of a preserved specimen of *Medusafissurella dubia* included branched coralline algae, suggesting that the diet of this species is comprised of encrusting algae, not unlike the diet of *Fissurella barbadensis* Gmelin, examined by Ward (1966). Thus, there is no indication that propodial development corresponds to an unusual diet in these species.

The two fissurelline genera having these propodial modifications occur in southern Africa and the western Indian Ocean, a region central to the distribution of genera in the subfamily. All five of the genera keyed above are known from South Africa. *Fissurella*, with its unmodified propodium, has more numerous species in the western hemisphere, on both sides of the Atlantic and in the eastern Pacific. *Amblychilepas*